

THE SUCCESSION OF *BELEMNOPSIS* IN THE LATE JURASSIC OF EASTERN INDONESIA

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ABSTRACT. Probably all the late Jurassic species of *Belemnopsis* from eastern Indonesia form part of the *moluccana* lineage which ranged from early Oxfordian to top Tithonian. *B. moluccana*, *B. galoi* and *B. stolleyi* appear in that order and form the main lineage, while *B. alfurica* and *B. mangolensis* represent impermanent branches with no descendants. Other previously recognized taxa are either synonyms, transitional forms or group names. Important morphological changes in the *moluccana* lineage include a decrease in guard length, forward movement of the point of maximum inflation and a decrease in dorso-ventral flattening. Stratigraphic distribution is established in the Misool Archipelago and Sula Islands and the relative stratigraphic position of many specimens or species described by earlier workers is inferred.

HISTORICAL PERSPECTIVE

Early research

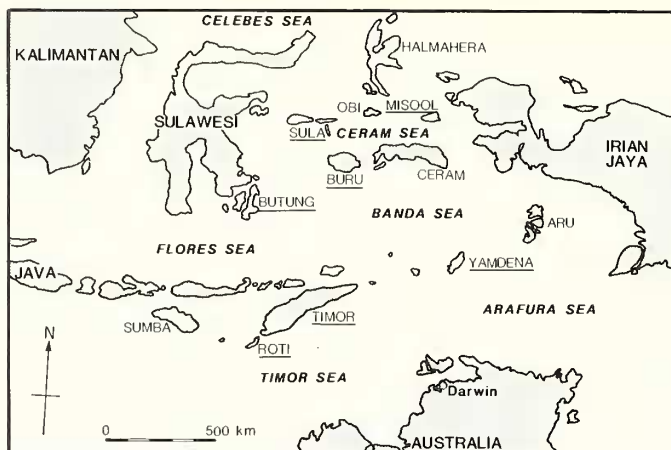
IN 1907 G. Boehm described a number of belemnites from Sula Islands and since that time the succession of *Belemnopsis* in the late Jurassic of Indonesia has exercised the minds of palaeontologists. Boehm (1907) recognized five species of *Belemnopsis* from Taliabu, the westernmost of the Sula Islands (text-fig. 1). *B. alfurica* (Boehm) was described mainly from specimens collected on the upper Wai Lagoi (Wai = river or stream) in eastern Taliabu and two specimens were recorded from Wai Galo, southeastern Taliabu. *B. galoi* (Boehm), *B. taliabutica* (Boehm), *B. sularum* (Boehm) and *B. moluccana* (Boehm) were described from Wai Galo, Safau (on the south coast of Taliabu), and 'Lagoi Mundung' (? = boulders from Wai Lagoi). Numerous other specimens were identified as *Belemnites* (= *Belemnopsis partim*) or compared with those named above. All figured specimens of *B. galoi*, *B. taliabutica*, *B. sularum* and *B. moluccana* (Boehm 1907) were collected from Wai Galo.

Although many specimens were available, Boehm's figures and descriptions are inadequate by today's standards. Discrete species cannot be recognized from his text or illustrations. He emphasized that interspecific differences were slight and was apparently in some doubt that all his species were valid (Boehm 1907). He later united *B. sularum* and *B. taliabutica* under *B. gerardi* Opper (Boehm 1912) but continued to regard *B. galoi* and probably *B. moluccana* as valid taxa.

Prior to Boehm's work, Rothpletz (1892) had identified *B. gerardi* from Roti and others subsequently recorded Boehm's five species, *B. gerardi*, and several new late Jurassic taxa from throughout eastern Indonesia (text-fig. 1).

Kruizinga (1920) studied material from Sula Islands, Roti and Timor. He united *B. moluccana*, *B. sularum*, *B. taliabutica* and *B. galoi* under *B. gerardi*, maintained *B. alfurica* as a distinct taxon, and described a new species, *B. indica* Kruizinga. He recognized that the latter was similar to specimens identified by Boehm as *B. moluccana*, but differed somewhat from Boehm's description (Kruizinga 1920). Other specimens were compared to *B. aucklandica* (Hochstetter).

Stolley (1929) examined collections from Misool, Timor, Yamdena, Roti and Buru. He recognized *B. moluccana*, *B. sularum*, *B. taliabutica*, *B. galoi*, *B. gerardi*, *B. indica*, *B. alfurica*, *B. aucklandica*, and identified *B. sp.* (aff. *tanganensis* Futterer) and *B. cf. hochstetteri* Hector. In 1935 he examined new collections made by Weber from Misool, identified many of his 1929 taxa, and recognized *B. indica-moluccana* and *B. incisa* as new species.



TEXT-FIG. 1. Eastern Indonesia. Members of the *moluccana* lineage have been recorded from the island groups with names underlined.

By 1940 some 50 papers, including the taxonomic studies cited above, had mentioned or discussed *Belemnopsis* from eastern Indonesia (Skwarko and Yusuf 1982). Many dealt wholly or partly with late Jurassic taxa and the species names quoted above had been widely used.

Modern work

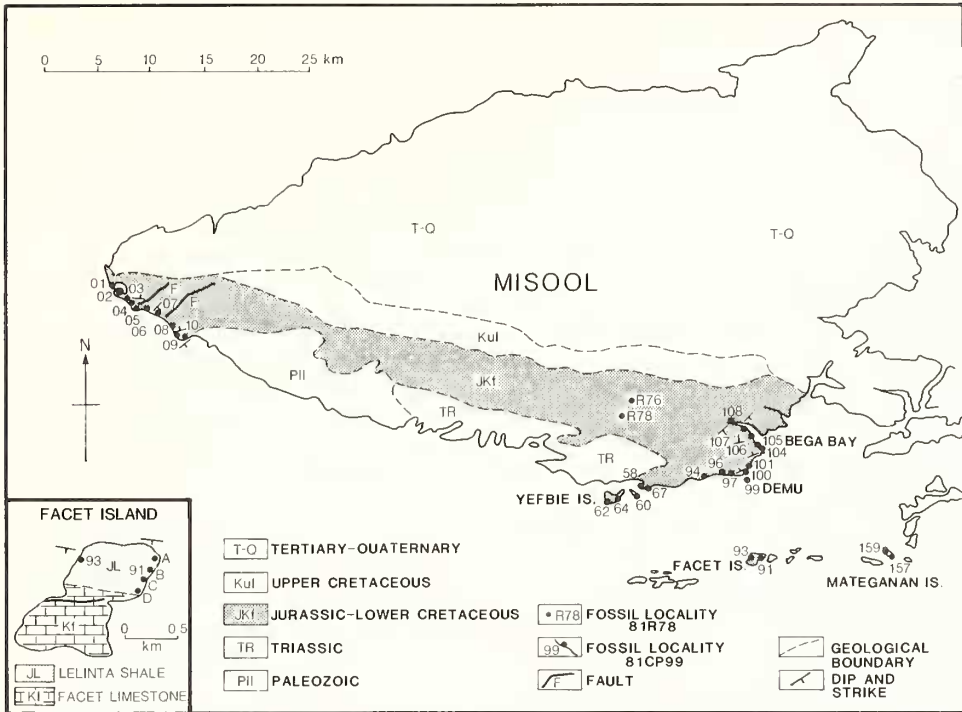
Stevens (1963*b*) re-examined *B. gerardi* Oppel and demonstrated that the name was valid for only two of Oppel's figured specimens (Oppel 1865, pl. 88, figs. 1, 2); the third (Oppel 1865, pl. 88, fig. 3) he included in a new taxon, *B. uhligi* Stevens. The latter was identified from India, Pakistan, Indonesia and New Guinea. Later Stevens re-examined Stolley's *B. aucklandica* and recognized part of the material (those specimens from Yamdena) as a new species, *B. stolleyi* Stevens (1964).

The Sula Islands were re-surveyed in 1976 (Sato *et al.* 1978) and provided the first reliable ages and relative stratigraphic positions for several late Jurassic species of *Belemnopsis*. Challinor and Skwarko (1982) examined the collections, identified and re-described *B. alfurica*, *B. moluccana*, *B. stolleyi*, and described five new taxa, *B. aucklandica galoi*, *B. a. similis*, *B. mangolensis*, *B. sp. B*, and *B. sp. C*. The Kimmeridgian belemnites were dated by bivalves; those from the Tithonian by ammonites (Challinor and Skwarko 1982, pp. 2-4).

B. stolleyi was found to be abundant throughout the late Tithonian; *B. moluccana* and the subspecies of *B. aucklandica* were abundant and appeared to have significant stratigraphic ranges in the Kimmeridgian and early Tithonian; *B. alfurica* and *B. mangolensis* abundant but of restricted stratigraphic horizon; *B. sp. B* and *B. sp. C* were represented by few specimens from single localities. Thus the sequence of late Jurassic *Belemnopsis* in Sula Islands was established, but stratigraphic ranges of all taxa could not be delimited and phylogenetic relationships remained obscure.

Misool Archipelago was re-surveyed in 1981 (Pigram *et al.* 1982) and study of the belemnites collected has been completed. Large numbers of late Jurassic *Belemnopsis* were collected from many horizons (text-fig. 2). Stratigraphic ranges and provisional ages have been established (Challinor in press *a*). Study of the new collections indicates that *B. moluccana*, *B. galoi*, *B. stolleyi*, *B. alfurica* and *B. mangolensis* are part of an evolutionary lineage which extends from early Oxfordian to late Tithonian time. All Indonesian late Jurassic *Belemnopsis* described by previous workers are apparently either species of the lineage or transitional forms appearing briefly between them.

The concept of an evolving lineage is not new. Both Stolley (1929) and Stevens (1965) suspected that relationships existed between a number of late Jurassic species but lacked reliable ages and a stratigraphic framework against which to view these relationships.



TEXT-FIG. 2. Fossil localities in Misool Archipelago from which members of the *moluccana* lineage were collected during the 1981 survey.

The group is discussed here under the name *moluccana* lineage. This paper compares the morphology of its species, examines changes which occur in the group, synonymizes nominal taxa considered identical to species of the lineage, and attempts to establish the stratigraphic position of specimens identified by earlier workers and now synonymized.

THE *MOLUCCANA* LINEAGE

The *moluccana* lineage is named from its first appearing species *B. moluccana* (Boehm). It includes five previously described species, *B. moluccana* (Boehm), *B. galo* (Boehm), *B. stolleyi* Stevens, *B. alfurica* (Boehm) and *B. mangolensis* Challinor, together with transitional forms. *B. moluccana*, *B. galo* and *B. stolleyi* have significant stratigraphic ranges and form a well-defined evolutionary lineage; *B. alfurica* and *B. mangolensis* appear briefly and are apparently divergent side branches of the lineage which left no descendants. Members of the group have been recorded widely throughout eastern Indonesia (text-fig. 1) either under the nomenclature recognized here or as synonyms and are also present in Papua New Guinea (Challinor in press *b*).

The earliest member, *B. moluccana*, first appears in the early Oxfordian (text-figs. 4, 7, 9) and is succeeded by *B. galo* (Boehm) in the early Tithonian. The latter is replaced in the middle Tithonian by *B. stolleyi* Stevens which extends into latest Tithonian beds. *B. alfurica* (Boehm) appears briefly in the Kimmeridgian and *B. mangolensis* Challinor briefly in the late Tithonian. Time stratigraphic subdivisions of the Indonesian late Jurassic are not precise and cannot be equated exactly with international subdivisions. Problems associated with ages of members of the *moluccana* lineage are discussed further elsewhere (Challinor in press *a, b*).

Boehm's original discussion of *B. moluccana* was based on five specimens from Wai Galo and three from other regions of Taliabu. His descriptive comments were minimal but his only figured

specimen (Boehm 1907, pl. 11, fig. 12a–b) is close to the concept of *moluccana* developed later by Stolley. Stolley's re-description of *moluccana* is based on numerous specimens from Misool and Yamdena. Its most characteristic features are a very prominent ventral groove, a strongly depressed cross-section and a hastate guard in which the widest point is situated in the apical half (Stolley 1929).

Challinor and Skwarko (1982) re-described *B. moluccana* from Wai Galo and from near Falabisahaya and Minaluli, Sula Islands. They confirmed the strongly depressed cross-section, but found that the widest point on the guard was situated at about the midpoint or slightly nearer the protoconch. Both the Wai Galo and Falabisahaya-Minaluli occurrences are near the top of the range of *B. moluccana* close to the point where transition to *B. galoi* occurs. Forward movement of the point of maximum transverse diameter is a critical feature of the *moluccana*–*galoi* transition.

Boehm's figured specimen of *B. galoi* (1907, pl. 10, fig. 5a, b) is subadult. This figure, together with his description of the guard as subcylindrical or slightly hastate with a 'round' cross-section (Boehm 1907, p. 72), establishes that his figured specimen is identical to subadult *B. galoi* studied here. Modern re-descriptions of *B. galoi* (Challinor in press a; Challinor and Skwarko 1982 under the synonyms *B. aucklandica galoi* and *B. a. similis*) establish the relationship of such subadult guards to fully mature specimens. The guard of *B. galoi* is very strongly grooved, moderately depressed to equidimensional in cross-section, slightly hastate and the point of maximum diameter is situated near the protoconch.

Stolley (1929) doubted that *galoi* was a valid and distinct taxon and suggested synonymy with *B. taliabutica* (Boehm). He recommended that the name *B. galoi* be applied to the specimen figured by Boehm (1907, pl. 11, fig. 4) as *B. cf. galoi*. This is not acceptable because the original of Boehm's pl. 11, fig. 4, cannot now be located and, more importantly, it is an approximately half grown specimen. Immature guards of Indo-Pacific *Belemnopsis* may be very different in morphology from adults of the same species.

B. stolleyi Stevens is based on specimens from Yamdena originally identified by Stolley (1929) as *B. aucklandica*. Stevens (1964) described a guard with a subconical non-hastate outline and profile, equidimensional cross-section, deep, narrow ventral groove and strong lateral lines. Challinor and Skwarko (1982) examined large collections of well-preserved *B. stolleyi* from Minaluli, Sula Islands. They confirmed the non-hastate outline and profile, equidimensional cross-section and strong lateral lines but found the ventral groove of many large specimens was wide and deep (Challinor and Skwarko 1982, pl. 16, fig. 8; pl. 17, fig. 6; pl. 18, fig. 6). A narrow groove was found mostly in immature guards and sometimes in the posterior region of large, strongly conical adults. The specimens on which Stevens' description is largely based (Stevens 1964, pl. 95) are mostly late immature guards and their deep, narrow grooves are at least partly a result of exfoliation (Challinor and Skwarko 1982) and partly due to their immaturity.

Boehm (1907) based his original description of *B. alfurica* on 86 specimens. He illustrated seven; four (1907, pl. 8, figs. 7–10) were very small juveniles; two (pl. 8, figs. 4, 5) immature adults; and one (pl. 8, fig. 11) a small apparently fully adult guard. His descriptive remarks were few, simply a comment on the very strong ventral groove and well defined lateral lines. His figured specimens were subsequently lost and Stevens (1963a) selected a lectotype from the remaining topotypes. Stolley (1929) discussed *B. alfurica* and identified Boehm's pl. 8, fig. 11, as *B. cf. alfurica*.

Boehm's specimens were collected from the upper reaches of Wai Lagoi, Taliabu, Sula Islands, but the river was not relocated by Sato *et al.* during the 1976 survey (S. K. Skwarko pers. comm.). However, they found many specimens of *B. alfurica* at the confluence of Wai Miha and Wai Betino in southern Taliabu. The collections contain small specimens similar to Boehm's figured juveniles, slender immature guards similar to Boehm's pl. 8, figs. 4 and 5, and to Stevens' lectotype, and specimens as large and larger than Boehm's pl. 8, fig. 11.

Challinor and Skwarko (1982) described the material and found that the guard of *B. alfurica* is cylindrical, sharply pointed, very slightly depressed in cross-section and has a wide, deep and long ventral groove.

B. mangolensis was first described in 1982 by Challinor and Skwarko from specimens collected

by Sato *et al.* (1978) near Minaluli, Mangole, Sula Islands. Its guard is relatively short and robust, depressed in cross-section, cylindrical or subconical with a strongly developed ventral groove.

Distribution of the Moluccana lineage in Misool Archipelago

Changes which occur during evolution of the *moluccana* lineage are viewed against stratigraphic distribution in Misool Archipelago (text-figs. 4, 7, 9). Misool contains the most extensive, complete and well known late Jurassic sequence in eastern Indonesia (Pigram *et al.* 1982). The Kimmeridgian–Tithonian of Sula Islands is also moderately extensive and well known (Sato *et al.* 1978; Challinor and Skwarko 1982), but the Oxfordian has yielded few belemnites and no members of the *moluccana* lineage except *Belemnopsis* sp. B. on the Oxfordian–Kimmeridgian boundary (Challinor and Skwarko 1982, text-fig. 3).

Late Jurassic lithology of Misool is detailed in Pigram *et al.* (1982, fig. 2) and briefly in text-figs. 4, 7, and 9 here. Fossil locality numbers in text-figs. 4, 7, and 9 preceded by 81CP are those occurring in the Misool sequence (details held in computer data record, Misool; program IJGMP, Geological Research and Development Centre, Bandung, Indonesia). Localities with alphanumeric designations (e.g. 8B, 2D) are from Sula Islands (details in Sato *et al.* 1978) and their stratigraphic relationships to adjacent 81CP localities are known only approximately.

Fossil localities within the Demu Formation provide adequate stratigraphic coverage of the unit although gaps from which no information is available are present in the lower and middle formation. Most of the Lelinta Shale is adequately covered; additional information is available from the Sula Islands from beds equivalent to those near the base and at the top of the formation. Data of particular value are available from the Sula Islands Kimmeridgian in beds where the transition from *B. moluccana* to *B. galoi* takes place. This interval is not exposed in Misool as far as is known but is well exposed on Wai Galo, Sula Islands. It includes the localities from which Boehm originally described *B. moluccana*, *B. sularum*, *B. taliabutica* and *B. galoi* (Challinor and Skwarko 1982).

B. moluccana appears near the base of the Demu Formation. It extends into the base of the Lelinta Shale where it is replaced by *B. galoi*, itself replaced by *B. stolleyi* in the upper half of the formation. *B. alfurica* and *B. mangolensis* were not found in Misool during the 1981 survey and they appear briefly in Sula Islands (Challinor and Skwarko 1982). The late Jurassic sequence of Misool is much condensed relative to that of Sula and if *B. alfurica* and *B. mangolensis* are present in Misool they must occur in sets of beds which have not been located.

EVIDENCE OF EVOLUTIONARY RELATIONSHIP

Evidence which indicates that most or all Indonesian late Jurassic *Belemnopsis* are part of an evolving lineage is based on their morphology and stratigraphic position. *B. moluccana*, *B. galoi*, *B. stolleyi*, *B. alfurica* and *B. mangolensis* are all large robust taxa similar in gross size and all are strongly grooved. They exhibit several unidirectional morphological trends. Those most evident are a reduction in the amount of dorso-ventral flattening, a reduction in postalveolar length and forward movement of the point of maximum width. Trends within the lineage are best shown by *B. moluccana*, *B. galoi* and *B. stolleyi*. *B. alfurica* and *B. mangolensis* appear briefly and either anticipate changes which occur later in the lineage or, in one instance, exhibit reversal of a character trend.

B. moluccana, *B. galoi* and *B. stolleyi* occur in stratigraphic succession without intervening gaps. Transitional forms which exhibit a mosaic of features present in species above and below occur in those stratigraphic intervals where transition occurs. If the group is accepted as a lineage these mosaics can be regarded as intermediate forms, but if the individual species are discrete taxa related only at generic level, then each morphologically distinct transitional form must also be regarded as a distinct taxon. This approach was adopted by earlier workers and is one of the reasons why such a diversity of names has been proposed within the group.

Two groups of characteristics can be recognized in species of the lineage. The first consists of

features common to all members and reflects the close relationships present. These characteristics are variable and better developed in some species, but variation is random and non-directional. The second group consists of features by which the individual species are recognized. Features in this group vary non-randomly with a number of unidirectional changes persisting throughout the lineage.

Morphological comparisons

(A) Randomly variable features. See plates 63–68.

Ventral groove. In all five species and in transitional forms the ventral groove is wide and deep. It commences at the alveolar rim and extends to within a few mm of the apex. All species include individuals in which the groove terminates further from the apex than in most and a few specimens in which it is wider or deeper than usual. In width, depth, and relations to guard diameters the groove is similar in all species (Challinor and Skwarko 1982, text-figs. 16, 21, 26, 33, 38). The groove of *B. moluccana* appears slightly wider and deeper than that of the remaining species but its guard is slightly more massive. Relative to guard diameters the groove is of similar proportions.

Groove width is at least partly correlated with guard development and in hastate immature specimens may be relatively narrow anteriorly. It is also partly correlated with guard cross-section and where this is equidimensional, and particularly where the guard is strongly conical and constricted as in the apical regions of some *B. stolleyi*, the groove may also be relatively narrow.

Apical configuration. In all species and transitional forms the sides of the guard at first converge gradually towards the apex; over the terminal 10–20 mm they converge more rapidly blunting the immediate apical region. This feature is best developed in late *B. moluccana* and *B. galoi*. A mucro may be present in all species; it is best developed in late *B. moluccana* and *B. galoi* and less marked and less regularly present in the others. However, in late members of *B. stolleyi* a very blunt, strongly mucronate apex is sometimes present. In all species the ventral surface of the immediate apical region is inflated to a greater or lesser degree, but this is most marked in late *B. moluccana* and *B. galoi*.

Lateral lines. Lateral lines are not usually prominent in adult Indo-Pacific *Belemnopsis* and are variably developed in species of the *moluccana* lineage. They are of similar configuration in all members; close together and well defined on the dorso-lateral surfaces of the apical region; less well defined, diverging slowly and passing down across the flanks of the mid region; ventrally placed anteriorly where they form a broad ventro-lateral depression. The ventral line is better defined than the dorsal. They are often clearly visible in *B. alfurica* and *B. stolleyi* and appear more strongly developed than in other members. However, in occasional specimens of *B. moluccana*, *B. galoi* and *B. mangolensis* they are clearly visible. They are more prominent in juvenile and immature guards of all species than in the adults.

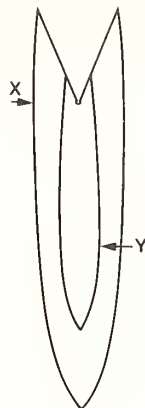
Apical line. The position of the apical line in relation to dorsal and ventral surfaces of the guard is similar in all species although apparently slightly more ventrally placed in *B. alfurica* and *B. stolleyi* (Challinor and Skwarko 1982, text-figs. 17, 22, 27, 34, 39).

(B) Morphological trends.

A small number of basic features or relationships determine the gross form of *Belemnopsis* and changes in these features strongly influence guard morphology. They include the position of maximum inflation of the guard, its length, and relationships between its diameters. These are the features which vary non-randomly within the lineage and, with one exception, they do so in a unidirectional manner.

Position of maximum transverse inflation. The position of the widest point on the guard determines its hastation characteristics and is important in specific recognition. However, it is variable within

TEXT-FIG. 3. Alteration in the position of maximum transverse diameter (W) during ontogeny in *Belemnopsis galoi*. Y indicates the position of W in a juvenile guard, X its position in an adult. Note contrasting outline of guards. Similar changes occur during ontogeny of all members of the *moluccana* lineage.



species and can only be determined reliably by examining many specimens. Furthermore, it alters in position during ontogeny, becoming more anteriorly placed as the guard matures. This is illustrated in text-fig. 3 where the outline of a large specimen of *B. galoi* has superimposed upon it the outline of an immature specimen. The points of greatest diameter (x and y) are widely separate producing contrasting outlines in immature and adult guards. Similar changes take place during the ontogeny of the other members of the lineage.

B. alfurica and *B. mangolensis* are essentially non-hastate, their guards being parallel-sided for most of their length. *B. moluccana*, *B. galoi* and *B. stolleyi* differ in hastation characteristics because the point of maximum inflation is situated differently. It is not always consistently placed in individuals of any one species due both to inherent variation and to incomplete ontogenic changes in specimens which are not fully mature, and is essentially a population feature.

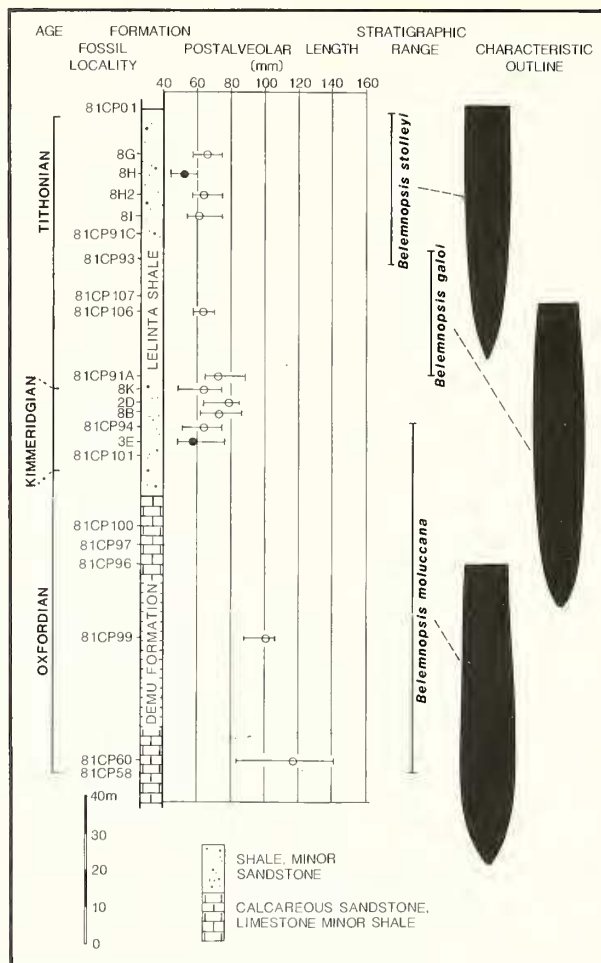
The original authors (or later workers) of the three species were quite specific about the position of maximum inflation. Stolley (1929) stated it was below the mid-point (i.e. situated towards the apex) in *B. moluccana*; Challinor and Skwarko (1982) found it to be anteriorly placed and near the protoconch in *B. aucklandica galoi* and *B. a. similis* (both taxa now considered true *B. galoi*, Challinor in press *a*); Stevens (1965) described the guard of *B. stolleyi* as non-hastate in outline and profile (i.e. the widest point is at the anterior limit). The outline of succeeding species of the lineage can be derived from that of preceding ones by forward movement of the point of maximum diameter. These changes are illustrated by slightly stylized diagrams in text-fig. 4.

B. moluccana first appears in Misool at locality 81CP58 near the base of the Demu Formation and its last appearance is in the lower Lelinta Shale (81CP94, 104). Throughout this interval specimens are typically moderately hastate and the widest point is situated near mid-guard or posteriorly (Pl. 63, figs. 1, 6, 11). No exposures of the interval between 81CP94 and 81CP91A are known and at the latter locality only *B. galoi* is present.

Beds which are apparently time equivalent to some of those in the interval between 81CP94 and 81CP91A are known from the Sula Islands (localities 2D, 8K, 8B, Challinor and Skwarko 1982, text-fig. 2). Only *B. moluccana* is present at 8B, *B. moluccana* and *B. galoi* are associated at 2D (although probably not at the same horizon) and only *B. galoi*, or *B. cf. galoi*, is present at 8K. Not all *B. moluccana* from these localities possess the characteristic outline of the taxon. In some the point of maximum transverse diameter has migrated towards the anterior or the guard is approximately parallel-sided (Pl. 64, fig. 1) but most specimens still retain the strongly depressed cross-section of *B. moluccana* (see below).

The first guards with the characteristic outline of *B. galoi* (i.e. widest point located near protoconch) are present at localities 81CP91A (Pl. 65, fig. 1) and 81CP105. Most adult guards collected between 81CP91A and 81CP106-7 have this form but at a slightly higher locality, 81CP93, a population which includes typical *B. galoi*, transitional forms and *B. stolleyi* is present.

Most specimens found between localities 81CP91C and 81CP01 are typical *B. stolleyi* but it must



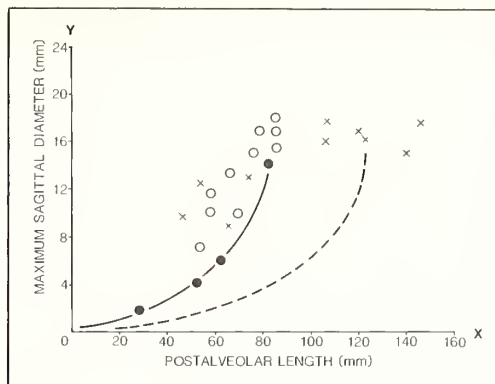
TEXT-FIG. 4. Reduction in postalveolar length during evolution of the *moluccana* lineage. 81CP localities from Misool Archipelago; others from Sula Islands. Relative stratigraphic position of Misool and Sula localities approximate; distributions viewed against stratigraphic column of Misool. Stratigraphic ranges of *B. moluccana*, *B. galoi* and *B. stolleyi* in Misool indicated. Interspecific changes in outline indicated by slightly stylized diagrams. Circles indicate mean value of postalveolar length, bars indicate range of values. Data from *B. alfurica* indicated by filled circle at locality 3E; from *B. mangolensis* by filled circle at locality 8H.

be emphasized that the characteristic outline of *B. stolleyi* (widest point at anterior limit) is present only in fully mature specimens. Immature guards in which the widest point has not migrated fully forward (Pl. 68, fig. 1) resemble mature specimens of *B. galoi* in outline.

B. alfurica appears suddenly at locality 3E and its cylindrical guard and near equidimensional cross-section contrasts markedly with the hastate strongly depressed *B. moluccana* from approximately equivalent horizons. Rare specimens with a moderately depressed cross-section (Pl. 64, fig. 13) are associated with *B. alfurica* at locality 3E and may be specimens transitional between *B. moluccana* and *B. alfurica*. In its non-hastate guard and equidimensional cross-section, *B. alfurica* anticipates features which become established later in the lineage, but *B. alfurica* itself does not persist and left no known descendants. It was apparently an unsuccessful evolutionary development.

B. mangolensis is known from a single locality, 8H, where it is associated with *B. stolleyi*. Abundant *B. stolleyi* occur stratigraphically above and below. The guard of *B. mangolensis* is

TEXT-FIG. 5. Growth pattern in *B. moluccana*. Open circles plot postalveolar length against maximum sagittal diameter in immature and adult specimens. Filled circles plot maximum sagittal diameter against postalveolar length for growth stages of a single guard. Growth curve by interpolation except for earliest stages. Crosses with X values between 100 and 150 mm are plots of postalveolar length against maximum sagittal diameter for early *B. moluccana*; the dashed line is a hypothetical curve for such a specimen. Crosses to the left of the solid growth curve are plots from immature guards from stratigraphic positions between 81CP99 and 81CP94 (see text-figs. 4 and 7).



cylindrical and in this respect is similar to individual *B. stolleyi*, but it differs in postalveolar length and cross-section. Like *B. alfurica*, *B. mangolensis* is present in only a narrow set of beds and left no descendants.

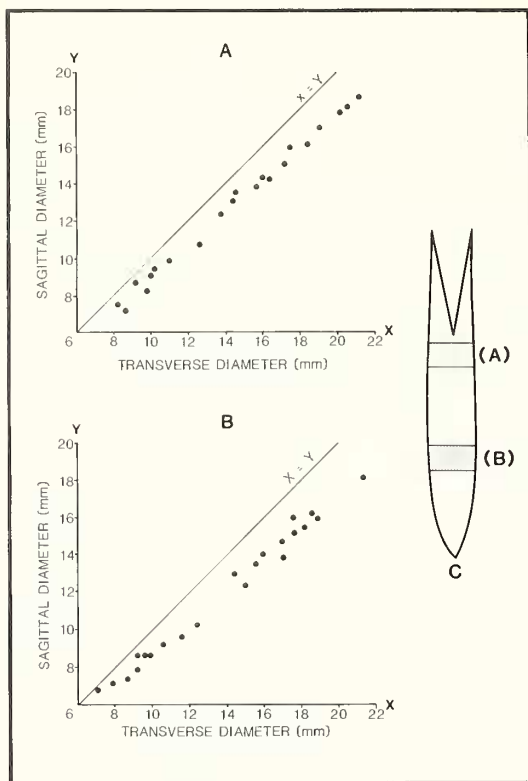
Guard length. Part of the alveolar region is missing in most belemnites and for this reason guard length is often expressed as postalveolar length or the relationship between postalveolar length and maximum diameter. Both features are relatively constant in adults of a given species.

The relationship between postalveolar length and maximum diameter in *B. moluccana* is illustrated in text-fig. 5. Open circles are observations from entire specimens; filled circles observations from well-marked growth stages within a single guard; the solid growth curve indicates changes in the length: diameter ratio during ontogeny. The dashed curve and observations indicated by crosses are discussed below.

Minimum, mean and maximum values of postalveolar length for all localities where sufficient data are available are indicated in text-fig. 4. Means are derived from between 3 and 22 observations. Throughout the ranges of *B. galoi* and *B. stolleyi* and at the top of the range of *B. moluccana* means vary from 58 to 80 mm. In the lower part of the *B. moluccana* range data are available from only two localities (81CP99 and 60); mean postalveolar length is 99 and 117 mm, respectively. Although mean length in early *B. moluccana* is clearly much greater than that of later members of the taxon and of other members of the lineage, not all specimens of early *moluccana* are long. In the shortest, postalveolar length approaches that of the longest specimens from higher in the sequence (text-fig. 4). It is not certain when reduction in length took place, but it probably occurred in mid-Oxfordian time.

The observations represented in text-fig. 5 by crosses near 120 mm on the x-axis are those from adult guards from localities 81CP60 and 81CP99. The dashed line is an estimated growth curve for a similar specimen and its shape is based on that of the plotted solid growth curve. No sufficiently complete adults were collected from between localities 81CP99 and 81CP101 to allow direct determination of postalveolar length in mature specimens from this interval. Several immature guards were found at localities 81CP96, 97 and 100; these are represented by crosses adjacent to the solid growth curve of text-fig. 5. If these young specimens are immature guards of long forms such as those from 81CP60 and 81CP99 they should plot close to the (hypothetical) dashed curve. Their location adjacent to the solid (observed) curve suggests they are immature guards of short forms. Long forms of *B. moluccana* may therefore be restricted to the lower part of its range.

The postalveolar length of *B. mangolensis* is clearly less than that of other members of the lineage and, because its diameter is similar, it is a more robust species. Length reduction in *B. mangolensis* continues a trend developed earlier in the lineage. *B. alfurica* is not significantly different in length from *B. galoi*, *B. stolleyi* and late *B. moluccana*.



TEXT-FIG. 6. Relationship between transverse and sagittal diameter in *B. moluccana*. A, observations from the anterior half of the guard; B, from the posterior half; C, approximate points of measurement for graphs A and B. Note that in both A and B, observation points diverge gradually from the line $X = Y$. This results from increasing depression of the cross-section as the guard matures. Note also that the observations in B are placed slightly further from the line $X = Y$ than in A, indicating that the cross-section is more depressed in the posterior half of the guard.

Relationship between diameters. Diametral relationships are probably the most consistent and stable feature of the guard of *Belemnopsis*. Diametral measurements are easily obtained and can be derived from fragmentary guards. In this paper relationship between diameters is expressed as the index of flattening A.

$$A = \frac{\text{Transverse diameter} \times 100}{\text{Sagittal diameter}}$$

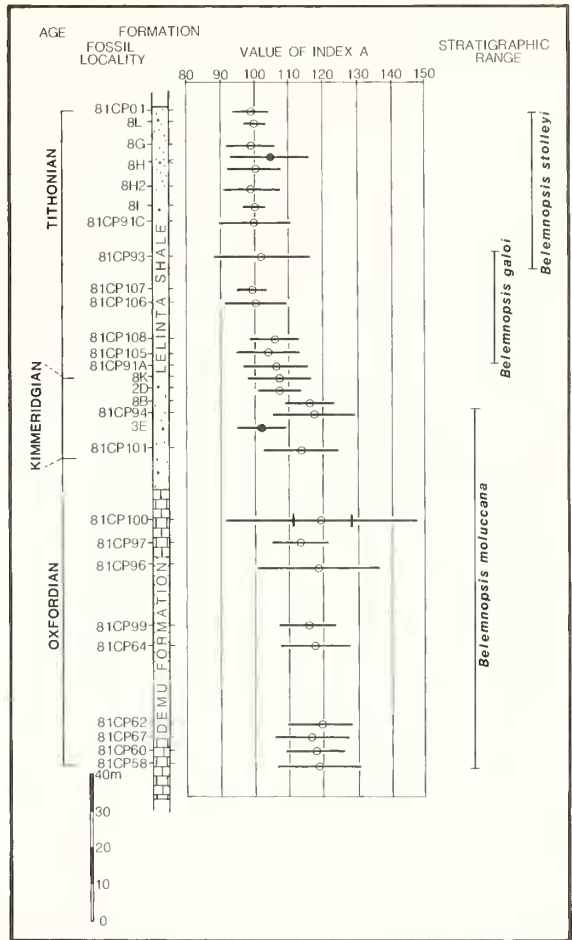
When diameters are equal, A has a value of 100. If transverse diameter is greater than sagittal (i.e. the guard is depressed in cross-section) A exceeds 100. When sagittal diameter is greater the guard is compressed and A is less than 100.

Taxonomic studies usually examine guard cross-sections at two or more points because diametral relationships differ at different points on the guard. They also change during ontogeny (text-fig. 6). For comparative purposes measurements should be made near the same point on the guard and on specimens of similar ontogenetic ages. Provided these conditions are observed, diametral relationships are remarkably stable within species and correlation coefficients as high as 0.98 have been recorded in other belemnite genera (Challinor 1975; Christensen 1974). To simplify presentation, diametral relationships are examined in this study at only one point about midway along the guard.

Mean values for A for each locality are indicated by circles in text-fig. 7. Horizontal bars indicate the approximate range of values for the population present at each locality and are arrived at by extending them $3\sigma-1$ each side of the sample mean. The very large (and probably false) approximate range of values at locality 81CP100 results from a sample of two specimens whose A values (indicated by vertical dashes on the range bar) are widely divergent. Means and approximate ranges at each locality are derived from between 2 and 32 observations.

Throughout the range of *B. moluccana* values remain relatively constant. Some variation between localities is evident and means range from 119 to 113 but high and low values are present

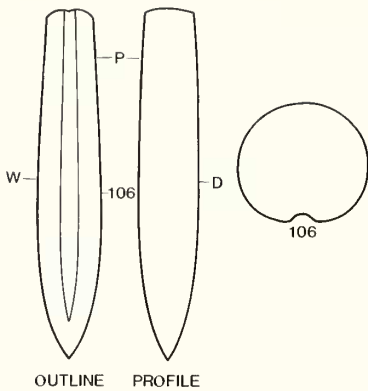
TEXT-FIG. 7. Reduction in value of the index A (relationship between diameters) during evolution of the *moluccana* lineage. 81CP localities from Misool Archipelago; others from Sula Islands. Relative stratigraphic position of Misool and Sula localities approximate; distributions viewed against stratigraphic column of Misool. Stratigraphic ranges of *B. moluccana*, *B. galoi* and *B. stolleyi* in Misool indicated. Circles indicate mean value of A at each locality; horizontal bars approximate range of values. Data from *B. alfurica* indicated by filled circle at 3E; from *B. mangolensis* by filled circle at 8H.



throughout the range. A sudden decrease in A occurs in the Misool sequence where transition from *B. moluccana* to *B. galoi* takes place. The value at the highest *B. moluccana* locality (81CP94) is 117, at the lowest *B. galoi* locality (81CP91A) 106. A similar transition takes place in the Sula Islands near Minaluli between localities 8B and 8K. *B. moluccana* from 8B have a mean A of 116. This locality contains *Retroceramus subhaasti* (Wandel) and '*Buchia*' sp. and is of approximately the same age as 81CP91A in Misool where *Malayomaorica malayomaorica* (Krumbeck) and *R. cf. haasti* (Hochstetter) are present. *B. galoi* from 8K has a mean A of 107. Although 8B and 8K are in different sections (Sato *et al.* 1978, fig. 7) 8K also contains *R. haasti* (Hochstetter) and '*Buchia*' sp. and must be stratigraphically close to 8B.

A collection from locality 2D, Wai Galo, contains *R. ?galoi* (Boehm), *M. malayomaorica* (Krumbeck), several *B. galoi* (mean A 107) and two specimens of *B. moluccana*, one with an A of 115, one with 109. This locality apparently represents the actual transition zone between *B. moluccana* and *B. galoi*.

Throughout the lower half of the range of *B. galoi* values of A remain close to 106 (localities 81CP91A, 105, 108, 2D, 8K); near the zone mid-point the value drops to near 100 (localities 81CP106, 107) and remains approximately the same throughout the remainder of the range of *B. galoi* and the whole of the range of *B. stolleyi*. Early members of *B. galoi* can be recognized by their moderately depressed cross-section; late members cannot be separated from *B. stolleyi* by cross-section characteristics alone.



TEXT-FIG. 8. Symbols, dimensions, specimen orientation, preparation, scale of illustrations in Plates 63-68. (P) Approximate position of protoconch. Determined by measuring the dorso-ventral diameter of the alveolus at the anterior break and locating the protoconch using the mean dorso-ventral alveolar angle of members of the *moluccana* lineage. (W) Approximate point of maximum transverse diameter. When the widest point is located within a region of approximately equal width, W is placed at its midpoint. (D) Approximate point of maximum sagittal diameter. (106) Value of the index A at indicated point on the guard or of illustrated cross-section. Long views photographed in ventral aspect (outline, ventral groove facing camera) and left lateral aspect (profile, ventral groove facing left). Scale. Long views $\times 1$. Transverse sections and apical views $\times 2$. Some specimens coated with ammonium chloride, some uncoated. IMC 472. Catalogue number of specimen held in the Indonesian Macropaleontology Collection, Geological Research and Development Centre, Bandung, Indonesia.

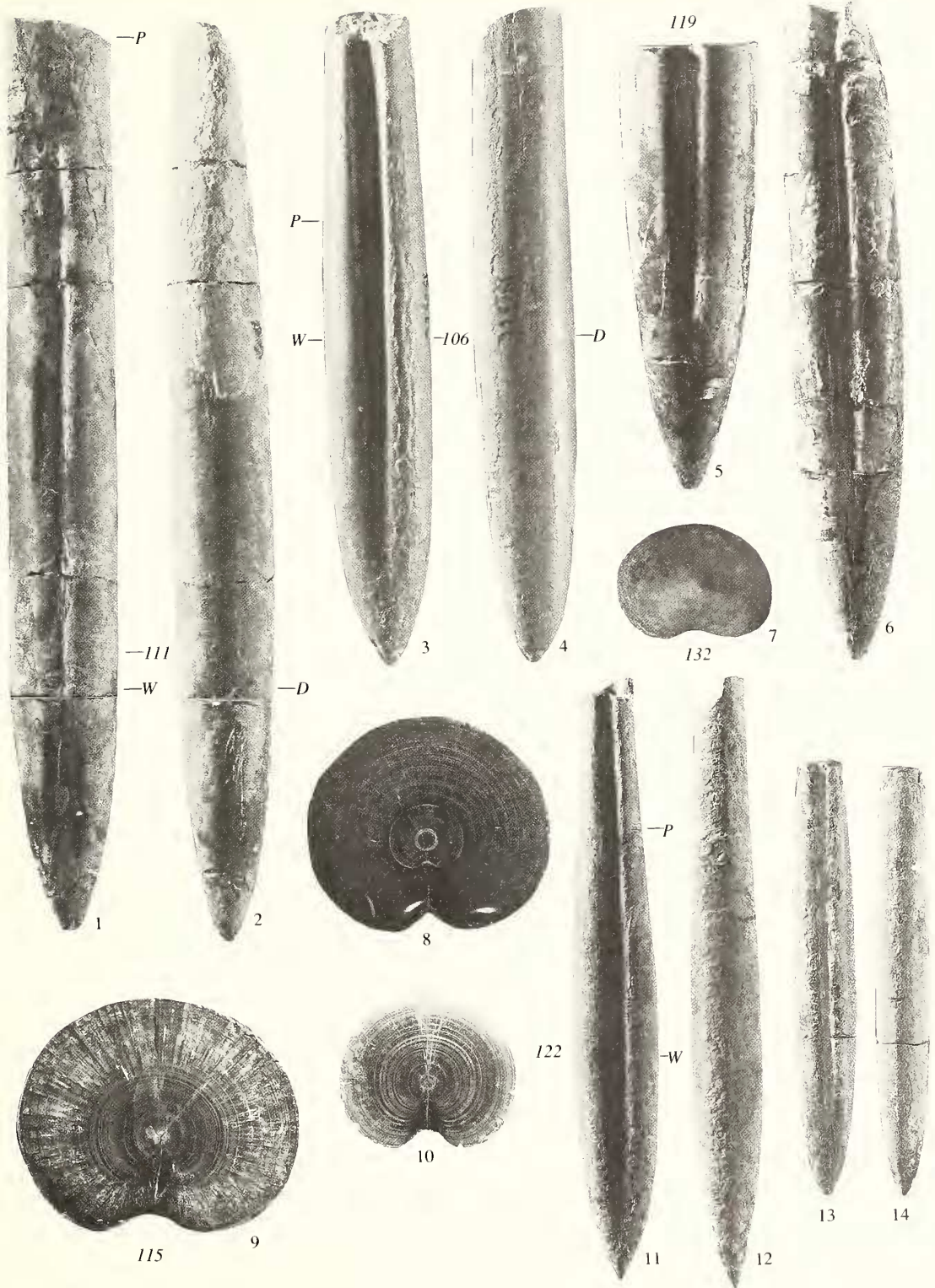
Both *B. alfurica* and *B. mangolensis* differ in values of mean A from other species of the lineage at or near their respective horizons. *B. alfurica* ($A = 102$) is significantly less depressed in cross-section than the contemporaneous *B. moluccana* but, as mentioned above, anticipates later developments within the group. On the other hand, *B. mangolensis* exhibits a reversal of the trend towards lower values of A. Its mean A of 105 is markedly greater than that of *B. stolleyi* ($A = 100$) below, at, and above its horizon, and is similar to that of early *B. galoi* much earlier in the lineage.

Profile of guard. Maximum transverse and sagittal diameters are usually almost coincident in *Belemnopsis*. When the position of maximum transverse diameter alters so does the position of maximum sagittal diameter. However, the profile of *Belemnopsis* is usually less hastate than the outline and sometimes non-hastate when the outline is significantly hastate.

EXPLANATION OF PLATE 63

Figs. 1-14. *Belemnopsis moluccana* (Boehm). 1, 2, IMC 472. Locality 81CP60, east of Yefbie Island, Misool, lower Demu Formation, early Oxfordian. 1, ventral, 2, left lateral, $\times 1$. 3, 4, J28281. Weber Collection, Natural History Museum, Basel, Switzerland, Yamdena, plaster cast, 3 ventral, 4 left lateral, $\times 1$. 5, IMC 479. Locality 81CP99, Demu Islands, Misool, middle Demu Formation, Oxfordian, ventral view, $\times 1$. 6, IMC 476. Locality 81CP99, Demu Islands, Misool, middle Demu Formation, Oxfordian, ventral view, $\times 1$. 7, IMC 480. Locality 81CP157, near Mateganan Island, Misool, lower Demu Formation, early Oxfordian, apical view, $\times 2$. 8, IMC 486. Locality 81CP96, Demu, Misool, lower Lelinta Shale, Oxfordian, transverse section, $\times 2$. 9, IMC 483. Locality 81CP94, Demu, Misool, lower Lelinta Shale, Oxfordian, transverse section, $\times 2$. 10 IMC 484. Locality 8B, Falabisahaya, Mangole, Sula Islands, Kimmeridgian, transverse section, $\times 2$. 11, 12, IMC 488. Locality 81CP104, Bega Bay, Misool, lower Lelinta Shale, Kimmeridgian, 11, ventral, 12 left lateral, $\times 1$. 13, 14, IMC 478. Locality 81CP159, near Mateganan Island, Misool, lower Demu Formation, early Oxfordian, 13, ventral, 14, left lateral, $\times 1$.

IMC 472, 478 and 480 are early members of the taxon. Note great length of IMC 472 and strongly depressed cross-section in IMC 480. J28281 was figured by Stolley (1929, pl. 3, fig. 1). Its horizon is unknown but morphology suggests it is of Kimmeridgian age. Its slightly depressed cross-section (if cast is a true replica), outline and profile are close to *B. galoi* (Boehm). Note regularly tapering somewhat elongate apical regions of IMC 476 and 479 typical of most members of the taxon. IMC 483, 484, 486 have typical cross-sections. IMC 488 is a strongly hastate, strongly depressed, immature guard.



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The profile of *B. moluccana* is usually less hastate than the outline; most specimens from the lower and middle parts of its range are hastate to some degree (Pl. 63, figs. 2 and 12). Non-hastate specimens appear near the top of the range; in these, dorsal and ventral surfaces are sub-parallel (Pl. 64, fig. 2).

B. galoi may be slightly hastate in profile and in these specimens dorsal and ventral surfaces converge slightly in the alveolar region (Pl. 65, figs. 2 and 7). Many are either cylindrical or subconical (Pl. 65, fig. 9). *B. stolleyi* is non-hastate in profile, often subconical (Pl. 66, fig. 10). Both *B. alfurica* (Pl. 64, figs. 6 and 9) and *B. mangolensis* (Pl. 68, figs. 6 and 12) are non-hastate in profile. Changes in profile are unidirectional and correlate with changes in outline, but are less marked.

It could be argued that differences between early and late morphs of *B. moluccana* and early and late morphs of *B. galoi* are as great as those between recognized species of the lineage, and that the morphs should be assigned at least subspecific status. There are practical difficulties involved in this approach. Early forms of *B. moluccana* in which the guard is long can only be recognized when all or at least most of the guard is preserved and this is frequently not the case. Cross-section differences between early and late *B. galoi* are apparent only at population level. Variation is such that less depressed members of early populations cannot be distinguished from more depressed members of later populations.

Juvenile and immature guards

Because they are usually hastate and the point of maximum diameter is situated further towards the apex than in adults, juvenile and immature guards differ in appearance from the corresponding adult. As a general statement very young specimens (e.g. Boehm 1907, pl. 8, figs. 7–10; Challinor and Skwarko 1982, pl. 14, figs. 1 and 2; and Pl. 65, figs. 10–13, Pl. 68, fig. 11 here) are impossible to identify as particular species unless they are accompanied by adults and it is difficult to be confident of many immature adults.

Young guards of *B. moluccana* can often be recognized from their strongly depressed cross-section and generally symmetrical and regularly curved outline (Pl. 63, fig. 13). Specimens from close to the point where the *B. moluccana*–*galoi* transition occurs may be more difficult to recognize, particularly if they are individuals in which the cross-section is not particularly depressed.

Many juvenile and immature *B. mangolensis* are relatively easily identified because their short

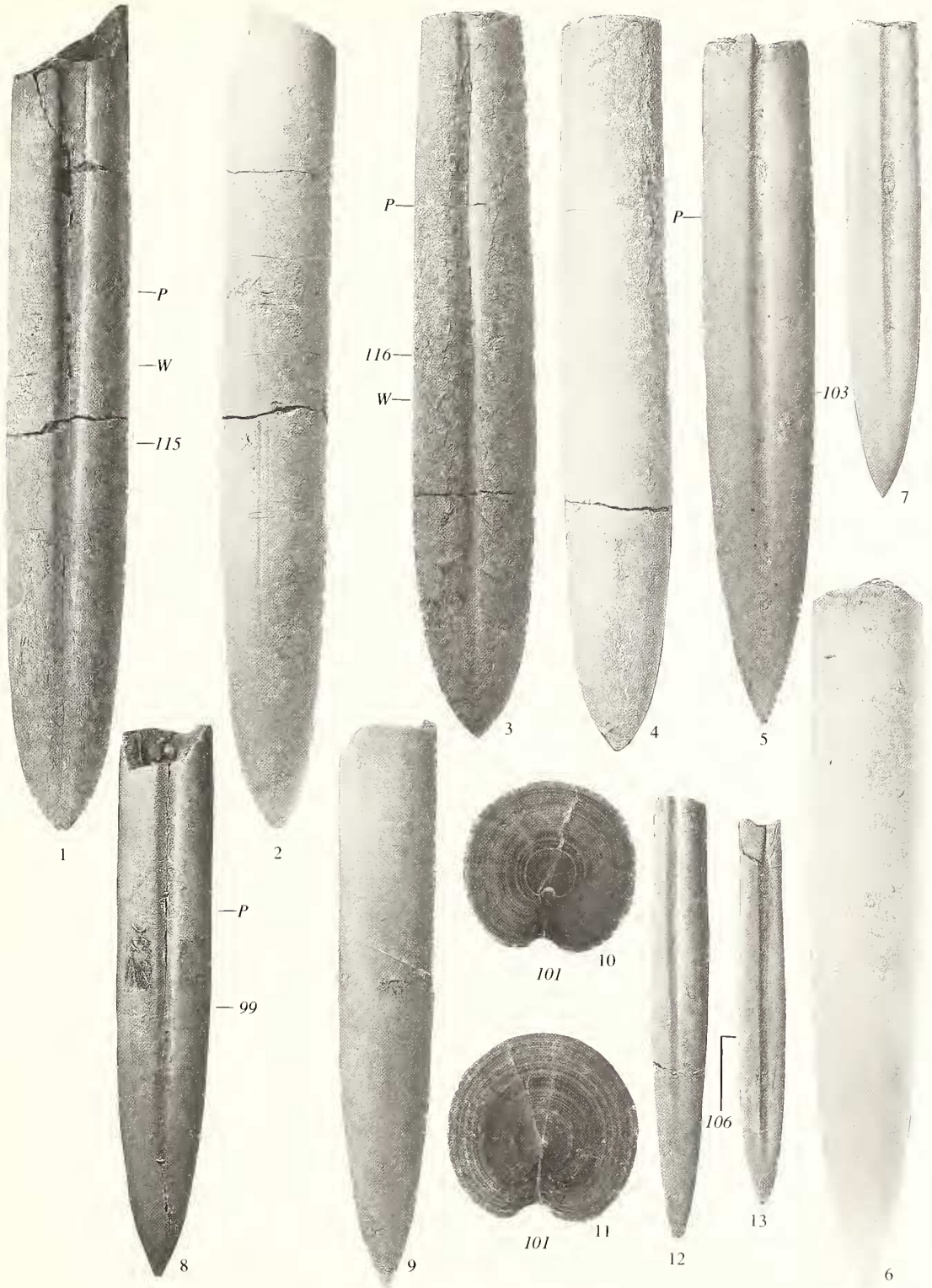
EXPLANATION OF PLATE 64

Figs. 1–4. *Belemnopsis moluccana* (Boehm), Kimmeridgian, Sula Islands. 1, 2, IMC 271. Locality 8B, Falabisahaya, Mangole, 1, ventral, 2, left lateral, $\times 1$. 3, 4, IMC 269. Locality 2D, Wai Galo, Taliabu, 3, ventral, 4, left lateral, $\times 1$.

Figs. 5–12. *Belemnopsis alfurica* (Boehm), Kimmeridgian, Sula Islands. 5, 6, IMC 254. Locality 3E₃, Wai Miha, Taliabu, 5, ventral, 6, left lateral, $\times 1$. 7, IMC 259. Locality 3E, Wai Miha, Taliabu, ventral view, $\times 1$. 8, 9, IMC 263. Locality 3E, Wai Miha, Taliabu, 8, ventral, 9, left lateral, $\times 1$. 10, IMC 550. Locality 3E, Wai Miha, Taliabu, transverse section, $\times 2$. 11, IMC 549. Locality 3E, Wai Miha, Taliabu, transverse section, $\times 2$. 12, IMC 262. Locality 3E₁, Wai Miha, Taliabu, ventral view, $\times 1$.

Fig. 13. *Belemnopsis* cf. *alfurica* (Boehm), Kimmeridgian, Sula Islands. IMC 258. Locality 3E, Wai Miha, Taliabu, ventral view, $\times 1$.

IMC 269 and 271 are late members of *B. moluccana* from close to the transition zone between *B. moluccana* and *B. galoi*. Note the blunt apex of both specimens and the subcylindrical outline and anterior position of the point of maximum diameter in IMC 271. The well-defined lateral lines are not typical. IMC 254 is a larger specimen of *B. alfurica* than those figured by Boehm (1907, pl. 8). IMC 263 is a similar sized but more robust specimen than Boehm's pl. 8, fig. 11b, IMC 259 a slightly hastate late immature guard; IMC 262 is similar to Boehm's pl. 8, Fig. 5b and the lectotype of Stevens (1963a, pl. 1, fig. 1). Note the quite different cross-section of IMC 549 and 550 and cylindrical, sharply pointed guard of the other *B. alfurica* compared with *B. moluccana* from nearby horizons. The hastate outline and depressed cross-section of IMC 258 suggest it may be transitional between *B. moluccana* and *B. alfurica*. IMC 258 was illustrated as *B. alfurica* (Boehm) by Challinor and Skwarko (1982).



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guards are comparatively robust, symmetrical in outline and quite strongly hastate (Pl. 68, figs. 13, 14). However, less strongly hastate specimens (Pl. 68, fig. 16) may be confused with other species. Their moderately depressed cross-section is a useful indication of identity if stratigraphic horizon is known.

Young guards of *B. alfurica* (Pl. 64, figs. 12 and 13), *B. galoi* (Pl. 65, figs. 10–13) and *B. stolleyi* (Pl. 67, figs. 10–12) present particular problems. Early *B. galoi* may sometimes be recognized from their cross-section (but may be confused with late *B. moluccana*) but apart from this, cross-sections are similar. All three species may vary in form from slender and elongate (Pl. 65, fig. 11) to more robust and hastate (Pl. 67, fig. 10) and the point of maximum diameter varies in position. The more slender and sharply pointed apical regions of *B. alfurica* and the sometimes more anteriorly placed widest point of *B. stolleyi* may be of value in assisting identification, but it is difficult to be objective when such slight differences in form are being evaluated.

TRANSITIONAL ZONES AND SPECIMENS

Major changes in form occur at four points on the *moluccana* lineage (text-figs. 4 and 7). The first occurs low in the range of *B. moluccana* and is marked by a substantial reduction in guard length. The second involves a change in diametral relationships and at approximately the same time the point of maximum diameter of the guard moves anteriorly. These two changes mark the appearance of *B. galoi* (text-figs. 4 and 7). The third is a further change in diametral relationships and occurs near the mid-point of the range of *B. galoi* (text-fig. 7). The fourth is a movement of the point of maximum diameter to the anterior limit of the guard; it takes place at the point where *B. stolleyi* appears (text-fig. 4).

The reduction in mean guard length early in the time range of *B. moluccana* is not well documented but it seems to take place in the Misool sequence somewhere above locality 81CP99 (text-fig. 4).

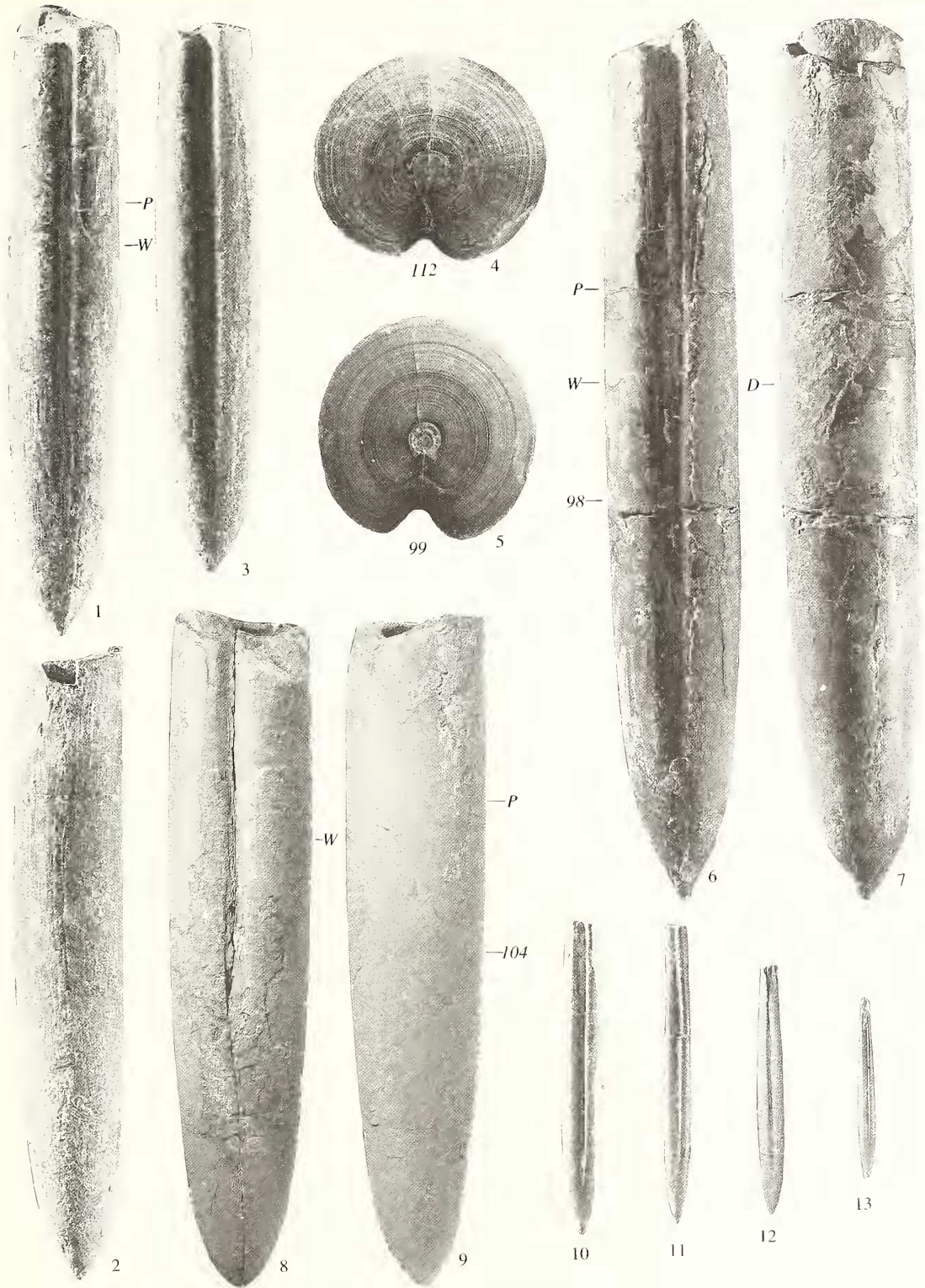
The changes which take place near the *B. moluccana*–*B. galoi* transition are among the most significant that occur during the lineage. The relevant stratigraphic interval is not well documented in Misool, but localities 8B, 2D, 8K, 3E, of Sula Islands are located within or near this interval. Evidence correlating these localities is mostly based on the common presence of *Retroceramus* and *Malayomaorica*, but stratigraphic and morphological evidence from members of the *moluccana* lineage also supports this placing.

Localities 2D and 8B include some 10 m of beds (Sato *et al.* 1978) and contain *B. moluccana* and *B. galoi* (2D) or *B. moluccana*–*B. galoi* transitionals (8B). Locality 8K includes *ca.* 50 m of beds and contains *B. moluccana*–*B. galoi* transitionals (Pl. 66, fig. 1) although most specimens are *B. galoi*

EXPLANATION OF PLATE 65

Figs. 1–13. *Belemnopsis galoi* (Boehm). 1, 2, IMC 500. Locality 81CP91A, Facet Island, Misool, Lelinta Shale, Tithonian, 1, ventral, 2, left lateral, $\times 1$. 3, IMC 513. Locality 81CP93, Facet Island, Misool, Lelinta Shale, Tithonian, ventral view, $\times 1$. 4, IMC 495. Locality 8K, Minaluli, Mangole, Sula Islands, Kimmeridgian, transverse section, $\times 2$. 5, IMC 524. Locality 81CP106, Bega Bay, Misool, Lelinta Shale, Tithonian, transverse section, $\times 2$. 6, 7, IMC 521. Locality 81R78, Upper Gam River, Misool, Lelinta Shale, Tithonian. 6, ventral, 7, left lateral, $\times 1$. 8, 9, IMC 291. Locality 8K, Minaluli, Mangole, Sula Islands, Kimmeridgian-Tithonian. 8, ventral, 9, left lateral, $\times 1$. 10, IMC 504. Locality 1C₁, Wai Kronci, Taliabu, Sula Islands, Tithonian, ventral view, $\times 1$. 11, IMC 505. Locality 8K, Minaluli, Mangole, Sula Islands, Tithonian, ventral view, $\times 1$. 12, IMC 289. Locality 8K, Minaluli, Mangole, Sula Islands, Tithonian, ventral view, $\times 1$. 13, IMC 507. Locality 81CP106, Bega Bay, Misool, Lelinta Shale, Tithonian, ventral view, $\times 1$.

IMC 289, 291, 494, 500 and 505 are early members of the taxon. IMC 507, 513, 521, 524 and probably 504 are late members. Note the moderately to strongly depressed cross-section of early forms and equidimensional cross-section of later forms. IMC 521 is a particularly large specimen but in outline and profile is similar to smaller specimens (c.g. IMC 513). IMC 291 resembles a specimen from Facet Island illustrated by Stevens (1963b, pl. 99, figs. 6–9) as *B. uhligi*.



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(Challinor and Skwarko 1982, pls. 13 and 14). A values for these localities are given in text-fig. 7. Locality 3E2 contains specimens similar to *B. galoi* in cross-section but like immature *B. moluccana* in outline and profile (those originally described as *B. sp. C*, Challinor and Skwarko 1982). *B. alfurica* is also present near this locality (text-fig. 9) and the *moluccana* lineage is particularly variable near this stratigraphic position.

Moderately or strongly depressed *B. galoi* occur in Misool at locality 81CP105 Bega Bay and 81CP91A Facet Island (text-figs. 2, 7). Both localities contain *Retroceramus* and *Malayomaorica* and the belemnite *Hibolithes compressus* Stolley. The latter is known only from 81CP105 and 81CP91A (Challinor in press *a*) and suggests close stratigraphic correlation between the localities. All known specimens which exhibit features transitional between *B. moluccana* and *B. galoi* are from beds which appear to represent a relatively short time interval. In Misool the transitional beds are located between 81CP94 and 81CP91A (some 15 m) suggesting that the changes which transform *B. moluccana* into *B. galoi* took place rapidly.

Eastern Facet Island contains a continuous uniformly dipping, but only partly exposed, section ca. 47 m thick in which the transition from *B. galoi* to *B. stolleyi* can be demonstrated. Locality 81CP91A at its northeastern corner (text-fig. 2) is the stratigraphically lowest known outcrop of Lelinta Shale on the island and spans some 10 m of beds containing well-preserved early *B. galoi* (Pl. 65, fig. 1). Successively higher horizons contain *B. galoi* and *B. galoi*—*B. stolleyi* transitionals (81CP91B, specimens mostly abraded float), abundant *B. stolleyi* and *Buchia* (81CP91C), and scattered *B. stolleyi* and inoceramids (81CP91D).

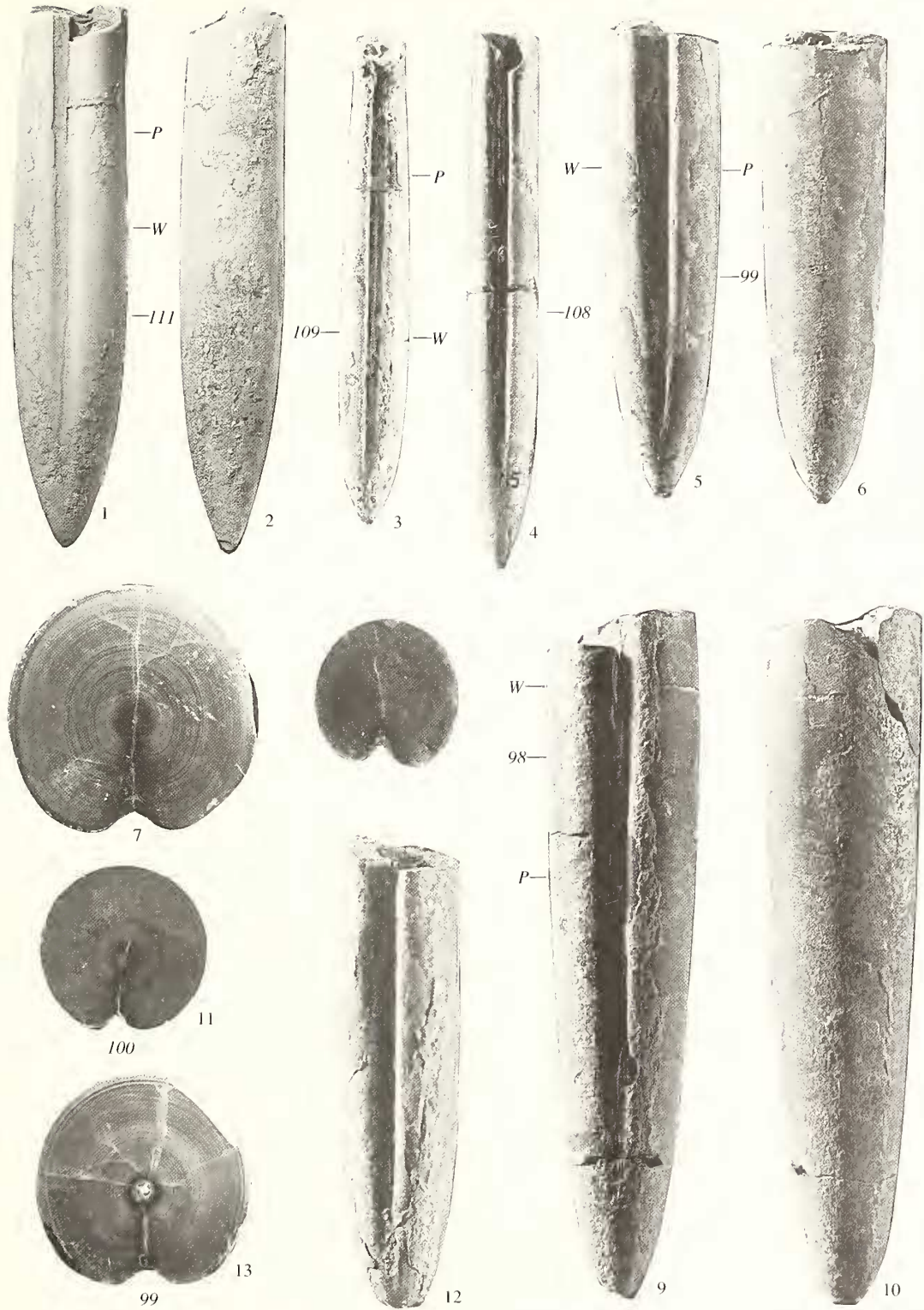
Locality 81CP93 on the northwest coast of Facet Island can be correlated with 81CP91B and C by its *Belemnopsis* and by the presence at the top of both sections of maroon *Buchia*-bearing siltstones. 81CP93 spans some 15 m of beds and contains well-preserved late *B. galoi* (Pl. 65, fig. 3) transitional forms (Pl. 66, figs. 4–6) and specimens which approach *B. stolleyi* in form (Pl. 66, fig. 12).

Transition from *B. moluccana* to early and late *B. galoi* can be demonstrated on the western side of Bega Bay (text-fig. 2, localities 81CP104, 105, 106) but higher beds containing *B. stolleyi* are not exposed and the section is complicated by folding. In western Misool (text-fig. 2, localities 81CP01–81CP10) transition from late *B. galoi* to *B. stolleyi* takes place in a sequence of calcareous

EXPLANATION OF PLATE 66

- Figs. 1, 2, 5, 6. *Belemnopsis* cf. *galoi* (Boehm). 1, 2, IMC 281. Locality 8K, Minaluli, Mangole, Sula Islands, ? Tithonian, 1, ventral, 2, left lateral, $\times 1$. 5, 6, IMC 518. Locality 81CP93, Facet Island, Misool, Lelinta Shale, Tithonian, 5 ventral, 6 left lateral, $\times 1$.
- Figs. 3, 4. *Belemnopsis galoi* (Boehm). 3, IMC 499. Locality 81CP91A, Facet Island, Misool, Lelinta Shale, Tithonian, ventral view, $\times 1$. 4, IMC 517. Locality 8K, Minaluli, Mangole, Sula Islands, ? Tithonian, ventral view, $\times 1$.
- Figs. 7, 8, 11, 12. *Belemnopsis* cf. *stolleyi* Stevens, Tithonian. 7, IMC 537. Locality 8I, Minaluli, Mangole, Sula Islands, transverse section, $\times 2$. 8, IMC 522. Locality 81CP91B, Facet Island, Misool, Lelinta Shale, transverse section, $\times 2$. 11, IMC 521. Locality 81CP91B, Facet Island, Misool, Lelinta Shale, transverse section, $\times 2$. 12, IMC 517. Locality 81CP93, Facet Island, Misool, Lelinta Shale, ventral view, $\times 1$.
- Figs. 9, 10, 13. *Belemnopsis stolleyi* Stevens. 9, 10, IMC 530. Locality 81R76, Upper Gam River, Misool, Lelinta Shale, Tithonian. 9, ventral, 10, left lateral, $\times 1$. 13, IMC 538. Locality 8G, Minaluli, Mangole, Sula Islands, Late Tithonian, transverse section, $\times 2$.

IMC 499 and 517 are immature early members of *B. galoi* both with moderately depressed cross-sections. IMC 281 resembles a specimen illustrated by Boehm (1907, pl. 11, fig. 10b) as *B. sularum*. The slightly hastate outline and blunted apical region of IMC 518 suggests *B. galoi*, but in general appearance the specimen approaches *B. stolleyi*. The stratigraphic position of IMC 521, 522 and 537 places them in or near the *B. galoi*—*B. stolleyi* transition zone and they are incomplete specimens difficult to assign with certainty to either species. IMC 517 approaches *B. stolleyi* in general appearance but its outline is *B. galoi*-like in some respects. IMC 530 is a particularly large fully conical specimen of *B. stolleyi* and IMC 538 is from high in the *B. stolleyi* zone of Sula.



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sandstones and siltstones. It is difficult to demonstrate convincingly due to structural complications and to poorly preserved specimens, a result of extraction from relatively hard sediments. No early *B. galoi* are known from western Misool.

Specimens transitional between *B. galoi* and *B. stolleyi* were not originally recognized in Sula Islands by Challinor and Skwarko (1982) but re-examination of collections from locality 8I reveals *B. galoi*-like forms, *B. galoi*-*B. stolleyi* transitionals and typical *B. stolleyi*. The transition zone in the Sula Islands is present between localities 8K and 8I south of Minaluli, somewhere within a section at least 120 m thick. The Tithonian sequence of Sula is very much thicker (ca. 520 m near Minaluli, Sato *et al.* 1978) than that of Misool (ca. 60 m on Facet Island) and contains many horizons with abundant *B. stolleyi* (Challinor and Skwarko 1982).

Changes in cross-section between early and late *B. galoi* appear to take place rapidly between localities 81CP108 and 106. However, most collections of early *B. galoi* contain a few relatively undepressed specimens and it is possible that this morphotype gradually increases in frequency throughout the lower range of *B. galoi*. Cross-section changes may in fact simply be a continuation of those which mark the transition from *B. moluccana* to early *B. galoi*.

In Misool changes in cross-section which occur between *B. moluccana* and late *B. galoi* take place throughout a stratigraphic interval which is only a small part of that of the whole *moluccana* lineage (text-fig. 7) and in these terms are relatively rapid. Changes in cross-section between *B. moluccana* and *B. alfurica* and changes in cross-section and length between *B. stolleyi* and *B. mangolensis* also seem to have been rapid. Most major changes in morphology during evolution of the lineage appear to have taken place relatively suddenly and are best interpreted in terms of the punctuated equilibrium model of evolution proposed by Eldredge and Gould (1972). A possible exception is the reduction in postalveolar length in early *B. moluccana*, which may have taken place more slowly but the evidence is not conclusive.

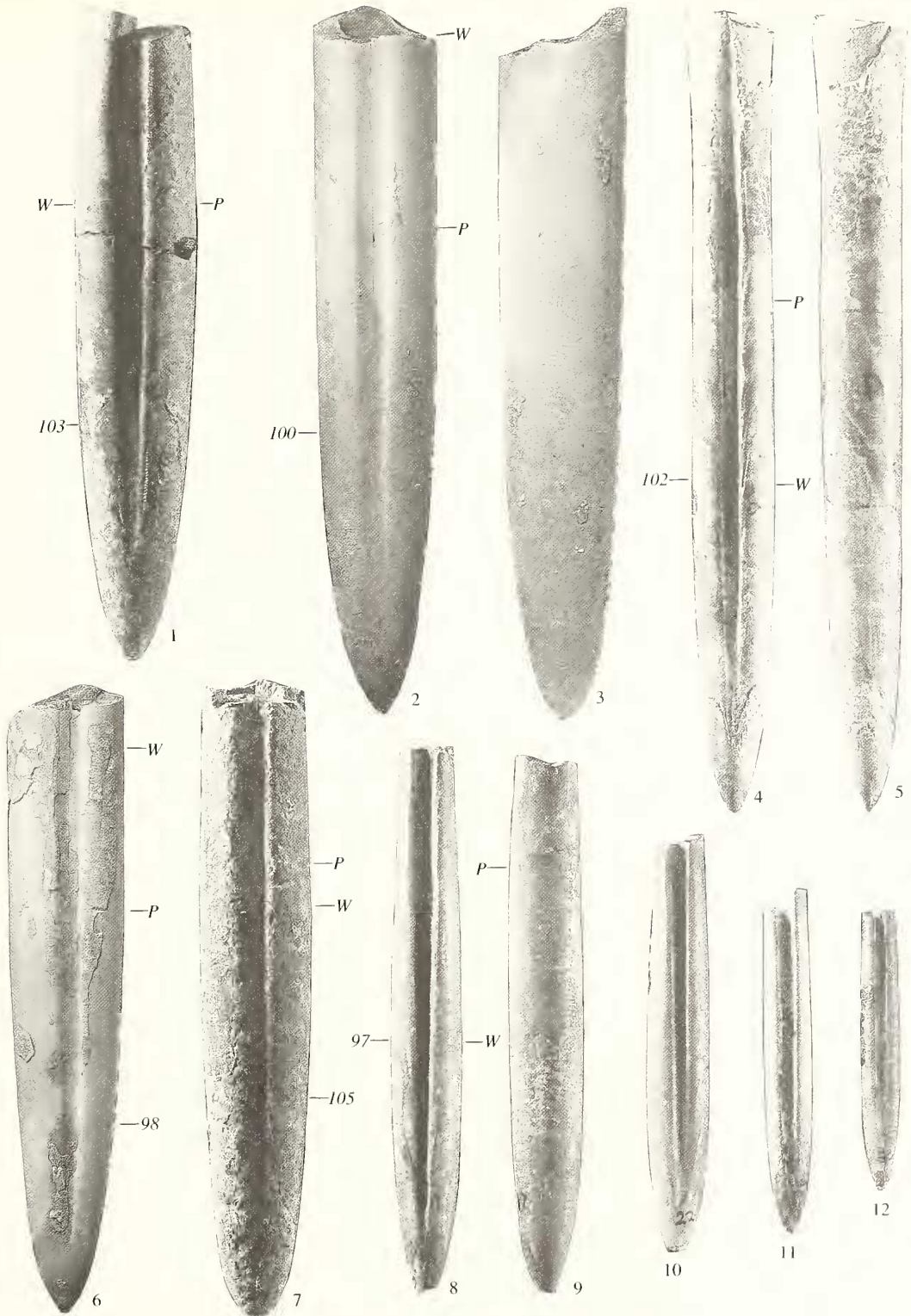
STRATIGRAPHIC POSITIONS OF EARLY COLLECTIONS

The stratigraphic position of taxa described or discussed by earlier workers and synonymous with members of the *moluccana* lineage can be assessed by evaluating morphology of their figured representatives and by considering comments on morphology, stratigraphic position and geographical locality by their authors. Morphology of figured specimens alone is not conclusive because usually few specimens are illustrated and a reliable indication of stratigraphic position can only be gained from the examination of reasonably large samples. Often geographic and stratigraphic information is not clearly stated by the original authors and interpretation is necessary.

EXPLANATION OF PLATE 67

- Fig. 1. *Belemnopsis* cf. *stolleyi* Stevens. IMC 535. Locality 81R76, Upper Gam River, Misool, Lelinta Shale, Tithonian, ventral view, $\times 1$.
 Figs. 2–12. *Belemnopsis stolleyi* Stevens, late Tithonian. 2, 3, IMC 303. Locality 8G, Minaluli, Mangole, Sula Islands, 2, ventral, 3, left lateral, $\times 1$. 4, 5, IMC 536. Locality 8H, Minaluli, Mangole, Sula Islands, 4, ventral, 5, left lateral, $\times 1$. 6, IMC 309. Locality 8G, Minaluli, Mangole, Sula Islands, ventral view, $\times 1$. 7, IMC 527. Locality 81CP91C, Facet Island, Upper Lelinta Shale, ventral view, $\times 1$. 8, 9, IMC 531. Locality 8H₂, Minaluli, Mangole, Sula Islands, 8, ventral, 9, left lateral, $\times 1$. 10, IMC 542. Locality 8H₂, Minaluli, Mangole, Sula Islands, ventral view, $\times 1$. 11, IMC 543. Locality 8H₂, Minaluli, Mangole, Sula Islands, ventral view, $\times 1$. 12, IMC 544. Locality 8H₂, Minaluli, Mangole, Sula Islands, ventral view, $\times 1$.

IMC 535 is a transitional form with postalveolar morphology of *B. stolleyi* but hastation features of *B. galoi*. IMC 303 is a fully adult *B. stolleyi* with a wide deep ventral groove. IMC 309 a similar sized specimen in which the groove narrows posteriorly. IMC 536 strongly resembles *B. cf. aucklandicus* of Kruizinga (1920, pl. 4, fig. 1a–d). IMC 527 is similar in size to the largest paratype of *B. stolleyi* (specimen J52/18, Stevens 1964, pl. 95, figs. 1–3). IMC 531, 542, 543, 544 are immature guards at various stages of development. Note strong similarities to juveniles of other members of the lineage.



CHALLINOR, *Belemmopsis*

The stratigraphic position of earlier described taxa relative to distribution of the *moluccana* lineage in Misool Archipelago is illustrated in text-fig. 9. Some positions are inferential. Few hard data exist even for specimens originally collected from Misool. No stratigraphic or geographical data are available for many specimens from other regions of Indonesia.

'Species' of earlier authors which occur within the ranges of *B. moluccana*, *B. galoi* and *B. stolleyi* are identical to the corresponding taxon. Species occurring between the ranges of *B. moluccana* and *B. galoi* (an apparent discontinuity resulting from inadequate exposure in Misool) are identical to one or other of those taxa or are forms transitional between them. A similar situation exists within the concurrent range interval of *B. galoi* and *B. stolleyi* where both taxa and transitional forms are present. A full discussion of synonymy within the *moluccana* lineage is presented elsewhere (Challinor in press *a*).

This attempt to define the stratigraphic position of earlier collections or specimens is based on my knowledge of the *moluccana* lineage in the Misool and Sula Islands sequences. It is not conclusive and makes no claim to be fully correct, but is perhaps the best interpretation available at present. Text-fig. 9 indicates that most early collections were made from beds high in the Upper Jurassic. Stevens (1965) considered his 'uhlgi complex' to be an indicator of the Kimmeridgian-Tithonian and the *moluccana* lineage is particularly abundant in beds of that age. Oxfordian representatives are less abundant in Misool and poorly recorded from Sula (Challinor in press *a*).

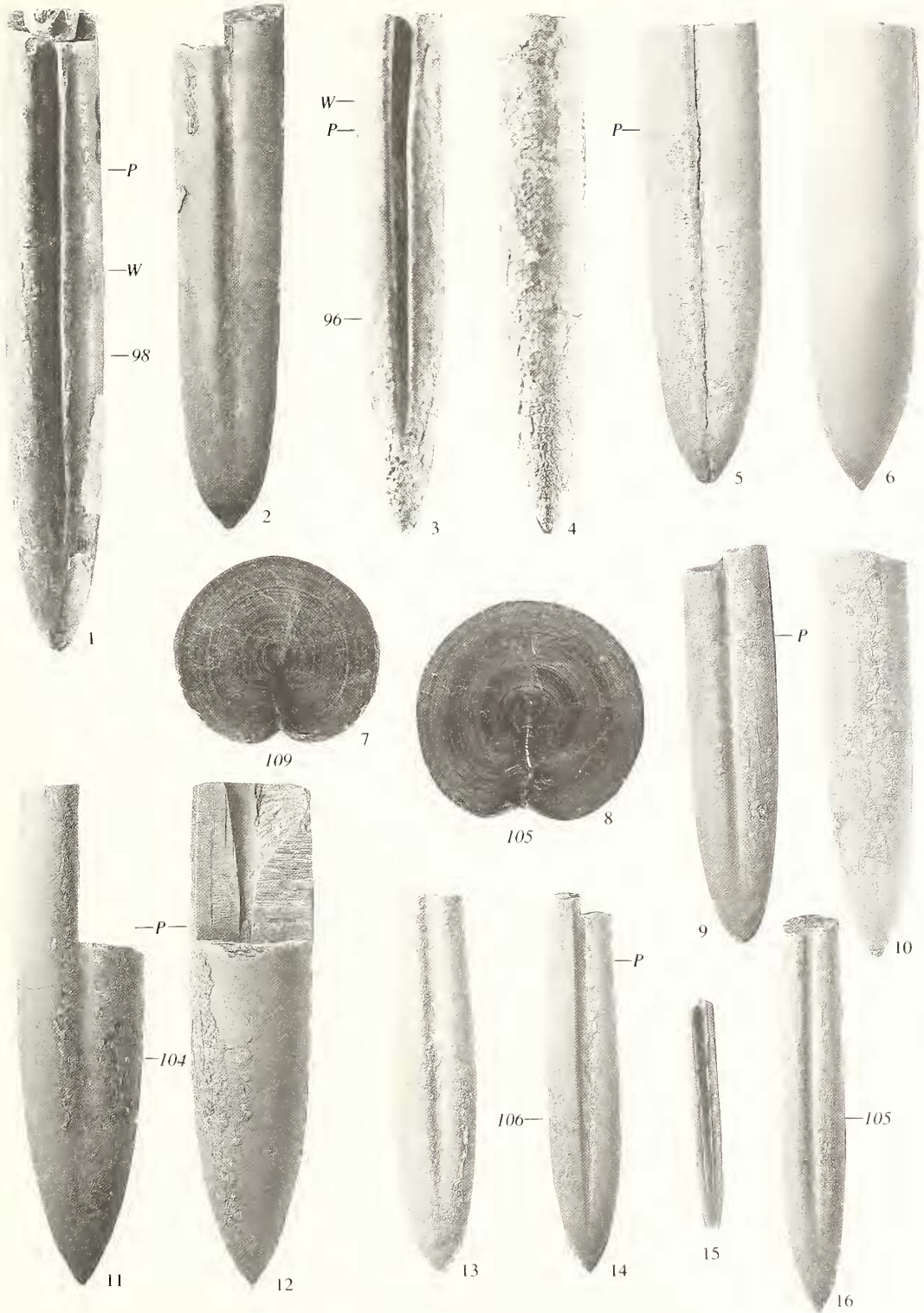
Specimens from the Demu Formation (and its time equivalents elsewhere) recognized as distinct species by earlier researchers are few (text-fig. 9). *B. moluccana* (Stolley 1929, pl. 3, fig. 5) and *B. indica* (Stolley) are long forms and such are known only from low in the range of *B. moluccana*. Collection localities of *B. indica-moluccana* and *B. taliabutica* (Stolley 1929, pl. 2, fig. 5) are known (Challinor in press *a*) but *B. moluccana* (Stolley 1929, pl. 2, figs. 9, 10, 12; pl. 3, figs. 3 and 4) and *B. indica* (Kruizinga) are positioned on morphology alone. Their position is speculative.

The stratigraphic positions of specimens from the lower Lelinta Shale (and its equivalents in Sula) from between the horizon of *B. sp. B* and locality 81CP91A are known (Challinor in press *a*). The group which contains *B. aff. tangansensis*, *B. cf. hochstetteri*, *B. moluccana* and *B. cf. sularum* (all of Stolley 1929) and *B. uhlgi* Stevens was collected from the lower Lelinta Shale (= Facet Shale of Stolley) on Facet Island (Challinor in press *a*).

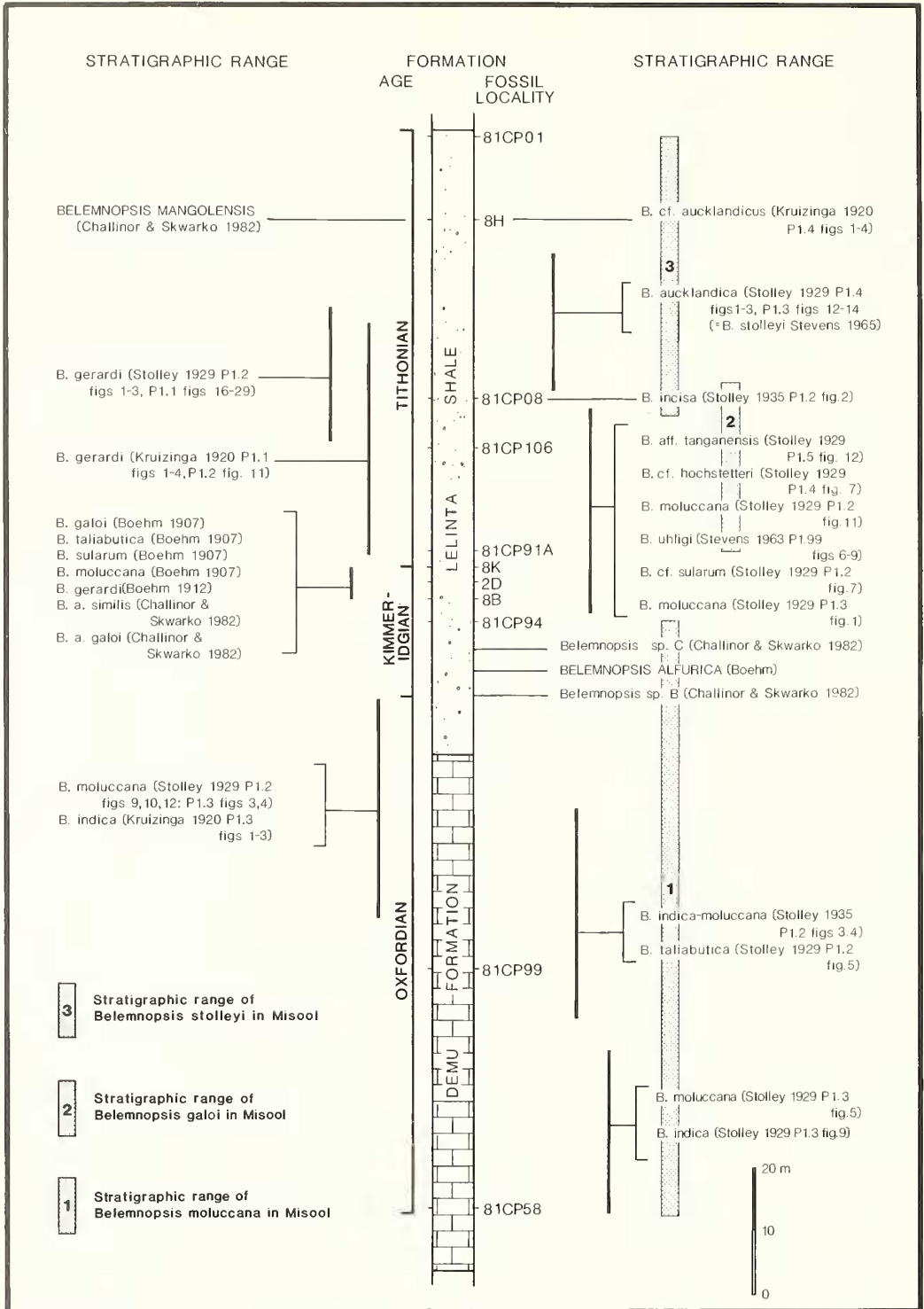
EXPLANATION OF PLATE 68

- Fig. 1. *Belemnopsis cf. galoi* (Boehm), IMC 543. Locality 8G, Minaluli, Mangole, Sula Islands, ventral view, $\times 1$.
 Fig. 2-4, 15. *Belemnopsis stolleyi* Stevens, late Tithonian. 2, IMC 308. Locality 8G, Minaluli, Mangole, Sula Islands, ventral view, $\times 1$. 3, 4, IMC 526. Locality 81CP91C, Facet Island, Misool, 3, ventral, 4, left lateral, $\times 1$. 15, IMC 546. Locality 8I, Minaluli, Mangole, Sula Islands, ventral view, $\times 1$.
 Figs. 5-14, 16. *Belemnopsis mangolensis* Challinor, Late Tithonian. 5, 6, IMC 322. Locality 8H, Minaluli, Mangole, Sula Islands, 5, ventral, 6, left lateral, $\times 1$. 7, IMC 548. Locality 8H, Minaluli, Mangole, Sula Islands, transverse section near midguard, $\times 2$. 8, IMC 547. Locality 8H, Minaluli, Mangole, Sula Islands, transverse section near midguard, $\times 2$. 9, 10, IMC 330. Locality 8I, Minaluli, Mangole, Sula Islands, 9, ventral, 10, left lateral, $\times 1$. 11, 12, IMC 321, Holotype. Locality 8H, Minaluli, Mangole, Sula Islands, 11, ventral, 12, left lateral, $\times 1$. 13, IMC 317. Locality 8H, Minaluli, Mangole, Sula Islands, ventral view, $\times 1$. 14, IMC 318. Locality 8H, Minaluli, Mangole, Sula Islands, ventral view, $\times 1$. 16, IMC 329. Locality 8H, Minaluli, Mangole, Sula Islands, ventral view, $\times 1$.

IMC 543 resembles *B. galoi* in hastation but *B. stolleyi* in postalveolar morphology. The blunt mucronate apex which occurs in a few *B. stolleyi* is present in IMC 308. IMC 526 is similar to a syntype of *B. stolleyi* (Stevens 1963*a*, pl. 95, figs. 10-12). IMC 546 can be identified as *B. stolleyi* only by its association with adult forms. IMC 322 is a *B. mangolensis* resembling some *B. galoi* (e.g. Challinor and Skwarko 1982, pl. 13, figs. 7-8) but its guard is shorter and sturdier. Both IMC 547 and 548 illustrate the depressed cross-section of *B. Mangolensis* similar to that of early *B. galoi*. Note contrasting cross-section of *B. stolleyi* from nearby horizons (e.g. Pl. 66, fig. 10). IMC 330 is a young adult *B. mangolensis* with a typically robust guard. Both IMC 317 and 318 illustrate the relatively distinctive outline of immature *B. mangolensis* but IMC 329, at a slightly earlier stage of growth, could readily be confused with other members of the lineage.



CHALLINOR, *Belemnopsis*



TEXT-FIG. 9. Approximate stratigraphic position of specimens or species discussed by earlier workers viewed against the stratigraphic column of Misool. Full details in text.

B. moluccana (Stolley 1929, pl. 3, fig. 1) from Yamdena approaches *B. galoi* in outline and its cross-section is only moderately depressed ($A = 106$). A cast of the specimen (Cat. No. J28281, Weber Collection, Natural History Museum, Basel, Switzerland) is illustrated here as Pl. 63, fig. 2. Its morphology suggests the specimen is transitional between *B. moluccana* and *B. galoi*.

B. gerardi (Stolley) was described from the Lelinta Shale on Facet Island and includes late *B. galoi*, transitional forms and *B. stolleyi*. *B. gerardi* (Kruizinga) is broader in concept and includes in addition early *B. galoi* (Challinor in press *a*). The horizon of *B. incisa* is known (Challinor in press *a*). *B. aucklandica* (Stolley) from Yamdena, later redescribed as *B. stolleyi* by Stevens (1964), are slightly depressed in cross-section ($A = 103$) indicating they are from low in the range of *B. stolleyi* or from the *B. galoi*-*B. stolleyi* transition zone. The horizon of *B. mangolensis* in the Sula Islands is known and specimens identical in appearance to *B. cf. aucklandicus* Kruizinga are present at the same locality (Challinor in press *a*).

STRATIGRAPHICALLY ADJACENT BELEMNOPSIS

Callovian, Oxfordian and earliest Cretaceous *Belemnopsis* which are not members of the *moluccana* lineage are known from eastern Indonesia (Challinor in press *a*). *B. persulcata* Stolley occurs in the early and mid Callovian and *B. wanneri* Stolley in the late Callovian and early Oxfordian of Misool. Specimens of *B. persulcata* are small (maximum length *ca.* 60 mm) with a narrow, deep, ventral groove and a very short dorsal alveolar groove. *B. wanneri* is moderately sized, cylindrical, slightly depressed in cross-section, has a relatively weakly developed ventral groove and an apical line which is only slightly ventrally placed. It is morphologically quite distinct from *B. moluccana*. *B. persulcata* is stratigraphically distinct from *B. moluccana*; *B. wanneri* is associated only with the earliest *B. moluccana*.

B. jonkeri Stolley appears in latest Tithonian or earliest Cretaceous beds of Misool and is present at the same locality (81CP01) as the latest *B. stolleyi*, but at a higher horizon. It differs from *B. stolleyi* in its larger size, wide, shallow, shorter, and highly variable ventral groove, slightly depressed cross-section and slightly ventrally placed apical line (Challinor in press *a*). To derive *B. jonkeri* from *B. stolleyi* requires reversal of several long-continued morphological trends and it is clearly distinct from the *moluccana* lineage.

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